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Expressing fear enhances sensory acquisition

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It has been proposed that facial expression production originates in sensory regulation. Here we demonstrate that facial expressions of fear are configured to enhance sensory acquisition. A statistical model of expression appearance revealed that fear and disgust expressions have opposite shape and surface reflectance features. We hypothesized that this reflects a fundamental antagonism serving to augment versus diminish sensory exposure. In keeping with this hypothesis, when subjects posed expressions of fear, they had a subjectively larger visual field, faster eye movements during target localization and an increase in nasal volume and air velocity during inspiration. The opposite pattern was found for disgust. Fear may therefore work to enhance perception, whereas disgust dampens it. These convergent results provide support for the Darwinian hypothesis that facial expressions are not arbitrary configurations for social communication, but rather, expressions may have originated in altering the sensory interface with the physical world.

Emotional facial expressions are known to be important in social communication[1–3], with research identifying vital information that can be inferred from these expressive actions[4] and demonstrating the consequences of facial displays for social interaction[5,6]. The biological importance of this putatively essential social capacity is supported by evidence from cross-cultural studies demonstrating cultural invariance in the recognition of expressions[7,8] and from affective neuroscience, which has demonstrated dedicated neural substrates for social perception of facial expressions[9]. Despite substantial evidence for the behavioral and neural bases of emotional expression recognition, little is known about expression production. In particular, why are emotional expressions associated with specific facial motor actions—that is, why do expressions appear precisely as they do?

One prominent theory of the neuroscience of emotion perception suggests that emotion recognition is specifically accomplished through mirroring motor actions to infer the mental states of others[9,10]. Because facial expression production is thought to trigger central representations of emotional experience[11,12], facial actions may facilitate expression recognition through mimicry, engaging common circuitry for generating and perceiving expressions[9]. Observing someone express an emotion would then result in an action and emotional resonance in the perceiver, resulting in shared emotional experience[13]. However, such behavioral and neural evidence does not address the origin of the precise physical appearance of expressions, leaving open the question of why specific muscle actions are associated with distinct emotional states[7,8].

A less appreciated theoretical account suggests that facial expressions not only express a mental state to be picked up by a perceiver, but also confer some other adaptive function for the sender. Consistent with the larger importance of emotions and motivation for organism survival, expressions may serve a more direct egocentric function. Expressions may prepare for or initiate actions that are appropriate for the emotion-eliciting situation[14]. Darwin suggested that facial expressions of emotion did not originate in nonverbal social communication, but in this less appreciated functional role[15], to modify preparedness for perception and action[16–18]. Facial configurations associated with different emotional states would serve to alter the sensory systems whose receptors reside on the face[16,18], augmenting or diminishing exposure to environmental stimulation.

We sought to address this sensory regulation hypothesis by examining two of Darwin's principles of facial expressive behavior: the principle of function, whereby specific facial expressions originate in action patterns serving adaptive information processing functions for the sender, and the principle of form, whereby emotions with opposite functions are opposites in facial action[15]. We specifically investigated the form and function of fear facial expressions in relation to the proposed role of fear in augmenting sensory vigilance[19,20]. Viewing fear expressions has been associated with enhanced behavioral and neural markers of attention and perceptual processing[21–24]. Here, we examined whether production of the facial motor actions of fear originated in a similar function. This was first accomplished by employing a visual statistical model of facial appearance to examine the action tendencies underlying and opposing fear expressions. These analyses revealed a physical opposition between fear and disgust, an emotion that is associated with sensory rejection[25]. We then used convergent methods to carry out detailed analyses of the functional consequences of fear and disgust facial actions for perception and action.

RESULTS

Fear expression form

Although facial expressions convey distinct emotional states[7], expressions are not structurally independent, containing systematic relations in their appearance[26,27]. As emotions are thought of as adaptive action

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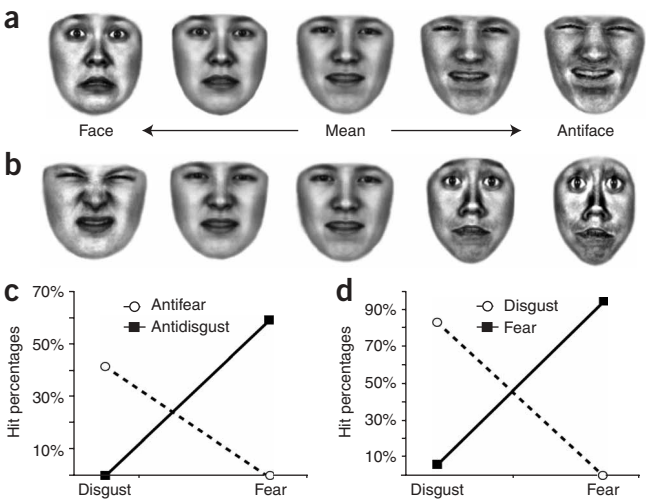

Figure 1 Fear, disgust and their associated antiprototypes defined in a multidimensional face space. (**a**) Expression trajectory between fear and antifear; each face corresponds to a location on the trajectory ranging left-to-right from +1.5 to –2.5 times the distance of the fear prototype to the average face. (**b**) Expression trajectory between disgust and antidisgust. (**c**) Hit percentages (*y* axis) for antifear and antidisgust faces on fear and disgust labels (*x* axis). A hit occurred when the rating for a given expression label was equal to the maximum rating for that face. (**d**) Hit percentages for fear and disgust prototypes.

tendencies, serving to prepare the organism for situation-appropriate actions[7,14,28], we hypothesized that expressions may serve to oppose each other's actions, and thus be opposite in form. To examine which action tendencies underlie fear facial expression form, we constructed expression prototypes of six basic emotions from a standard cross-cultural dataset[29] using a well-known computer graphics model of facial appearance[30] (see Methods). The model represents each face in the dataset as a vector in a multidimensional space coding variations in shape and surface reflectance. Expression prototypes were created by averaging the vector representations of all exemplars in an expression category. We created expressions by varying the vector representations of the fear prototype along an expression trajectory that ranged from prototypical fear to its associated antiprototype, a face containing opposing shape and surface reflectance features from the fear prototype[31] (**Fig. 1a**). The expression trajectory was generated by weighting the prototype vector either positively (toward the prototype) or negatively (toward the antiprototype) and synthesizing faces at successive intervals along the trajectory.

We found that fear antiprototypes in this multidimensional face space were most similar in structure to disgust ($r = 0.69$). Furthermore, when participants were tested on expression recognition, the fear antiprototype (**Fig. 1a**) was rated maximally as disgust relative to other emotion labels, suggesting fear facial actions oppose disgust. To examine whether disgust prototypes also oppose fear, we visualized the trajectory between disgust and its associated antiprototype (**Fig. 1b**). Disgust antiprototypes in this multidimensional face space were closest to fear ($r = 0.69$) and surprise ($r = 0.70$). When participants were tested on expression recognition, the disgust antiprototype (**Fig. 1b**) was rated maximally as fear, with the ratings of fear and disgust for the antiprototypes resulting in a highly reliable crossover interaction ($F_{1,17} = 25.47$, $P < 0.001$; **Fig. 1c**). A corresponding analysis of fear and disgust prototypes revealed an identical crossover interaction as that of the antidisgust and antifear prototypes ($F_{1,17} = 109.63$, $P < 0.001$; **Fig. 1d**).

To better understand this opposition in appearance, we next visualized the action patterns underlying opposition in fear and disgust facial expressions. Vector flow fields were derived from the surface deformations of fear and disgust from their antiprototypes. The vector flow fields demonstrated a spreading, rather than contracting, longitudinal action for fear (**Fig. 2a**) compared with disgust (**Fig. 2b**). This conjunctive spreading versus contracting of the radiating muscular frames circling the mouth, nose and eyes may serve a primitive capacity to regulate sensory exposure[16,17]. In sum, the facial appearance of fear, an emotion associated with sensory vigilance[19,20], appeared to oppose that of disgust, an emotion associated with sensory rejection[25]. These results suggest that these two distinct social signals of emotional states have been shaped, at least in part, by opposing underlying action tendencies related to sensory regulation.

Fear expression function

If opposition in fear-disgust expression form indeed reflects evolutionarily adaptive action tendencies, then these expressions should retain some residue of this function, despite their present day use as social signals. We conducted a series of studies testing the appearance model's predictions on measures of sensory regulation.

Consistent with the importance of the eyes in fear facial expression recognition[32,33], the appearance model revealed that fear and disgust expressions opposed each other in terms of eye and brow features, with fear resulting in eye-lid opening and brow raising, and disgust in eye closing and brow lowering (**Figs. 2** and **3**). We examined the functional influence of fear and disgust expressions on visual-field size by employing a psychophysical magnitude–estimation procedure. Participants were positioned closely in front of a large wall-mounted grid and were asked to judge the size of their visual field relative to posing neutral expressions along horizontal, vertical and two oblique meridians during a directed facial-action task in which participants posed fear and disgust (see Methods). Expression was shown to significantly influence visual-field size ($F_{2,19} = 15.43$, $P < 0.0001$; **Fig. 3a**,**b**). Consistent with increased sensory vigilance, fear resulted in a substantially larger subjective visual field relative to disgust ($F_{1,19} = 30.80$, $P < 0.0001$), as well as an increase relative to neutral baseline ($F_{1,19} = 6.67$, $P < 0.02$). The opposing actions in disgust resulted in a significant reduction in visual-field size relative to neutral baseline ($F_{1,19} = 8.81$, $P < 0.006$). The effect of expression on visual-field size depended on visual-field location ($F_{14,266} = 9.09$, $P < 0.0001$). Fear resulted in a

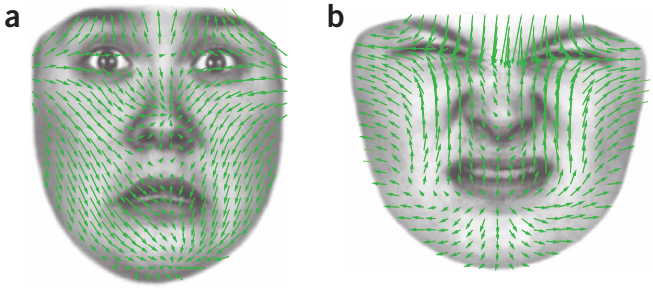

Figure 2 Opposition in facial actions between fear and disgust expressions. (**a**,**b**) Green arrows depict vector flow fields of skin surface deformations stemming from the antiprototype to the corresponding expression prototype, allowing visualization of the underlying facial-action patterns. Vector flow from antifear to fear (**a**) and antidisgust to disgust (**b**) indicated the opposing expansion versus compression along the longitudinal axis emanating from the bridge of the nose. This resulted in raised versus lowered brows, increased versus decreased eye aperture and vertical elongation versus compression of the nose associated with raised versus lowered lips.

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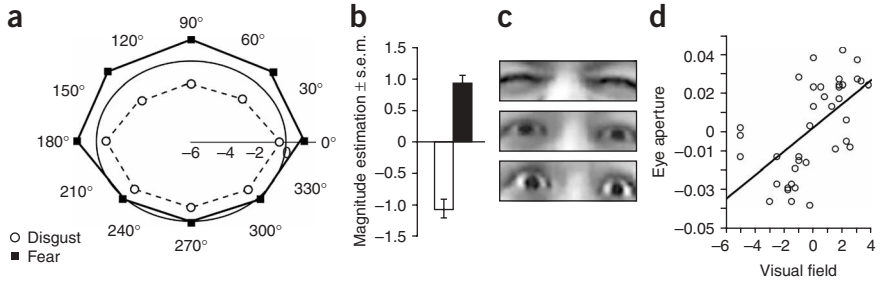

Figure 3 Subjective visual-field changes for participants posing fear and disgust expressions. (**a**) Changes in visual field estimation along horizontal, vertical and oblique axes. Central ellipse is neutral baseline. Unit markings are in 9.5° of visual angle. (**b**) Change in estimated visual-field size (in standardized units) for fear and disgust expressions relative to neutral expressions, averaged across visual-field location. (**c**) Average eye opening from participants posing disgust, neutral and fear expressions (from top to bottom row). (**d**) Correlation of vertical eye-size measurements of participants posing disgust and fear expressions with upper visual-field magnitude change from neutral.

marked increase in the upper ($F_{1,266} = 174.70$, $P < 0.0001$), but not the lower visual field ($F_{1,266} = 1.13$, $P > 0.29$), consistent with the brow and upper eye-lid raise (**Figs. 2a** and **3**). In contrast, disgust resulted in a decrease in the upper ($F_{1,266} = 113.51$, $P < 0.0001$) and lower fields ($F_{1,266} = 50.05$, $P < 0.0001$), consistent with brow lowering and upper cheek raise (**Figs. 2b** and **3**). Fear's enhancement only for the upper visual field may be argued as having limited functional importance. However, the lower visual field under neutral viewing conditions more closely approximates complete coverage, whereas the upper visual field is substantially more restrictive, in part reflecting occlusion from the eyelid and brow[34]. The functional importance of fear expressions may reflect the retraction of these anatomical features, affording a more complete visual field.

We next examined whether changes in estimated visual field size were specifically related to the changes in physical differences in eye aperture that are associated with expression generation. Eye regions were outlined from film clips taken during the directed facial action task (see Methods) to determine the extent of eye opening in each participant. As predicted, fear expressions resulted in greater vertical eye opening relative to disgust ($F_{1,18} = 148.08$, $P < 0.0001$). We next used the physical distance between participants' lower and upper lids to predict their visual-field size by correlating it with visual-field changes along the vertical meridian (**Fig. 3d**). Vertical eye aperture correlated significantly with perceived changes in the upper visual field ($r = 0.593$, $t(18) = 4.41$, $P < 0.001$). These results show that the antagonistic eye opening and closing associated with fear and disgust regulate visual-field size.

Fear may induce subjective changes in visual-field perception, but a stronger test of sensory vigilance is to show that peripheral stimulus detection is altered by expression. To corroborate the subjective results, we applied an objective visual perimetry procedure in an additional experiment to test stimulus detection–eccentricity thresholds at upper horizontal, oblique and vertical meridians while participants posed fear, neutral and disgust facial configurations (see Methods). Stimulus detection differed with respect to expression condition ($F_{2,26} = 28.675$, $P < 0.001$), with the effect of expression depending on visual-field location ($F_{8,104} = 14.856$, $P < 0.001$). Specifically, in the fear condition, participants detected objects at farther eccentricities than in the neutral condition for the upper visual field ($F_{1,104} = 84.182$, $P < 0.001$), but not for the horizontal meridian ($F_{1,104} = 0.802$, $P = 0.373$). Conversely, stimulus detection in the upper visual field was reduced for disgust relative to neutral ($F_{1,104} = 105.909$, $P < 0.001$), but not for the horizontal meridian ($F_{1,104} = 1.829$, $P = 0.179$). An analysis of catch trials in which no stimulus was present did not reveal any differences in response bias across expression types (Friedman test, $\chi^2(3) = 0.931$, $P = 0.818$). In sum, these results demonstrate that fear expressions enhance and disgust expressions reduce stimulus detection in the upper visual field, consistent with opposing eye lid and brow actions regulating retinal exposure[35].

Eye opening and brow raising in fear may reflect not only altered functional visual-field size, but also multiple functional benefits, affording a more effective sampling of the entire visual field. Eye movements are instrumental in acquiring information from the visual field, and fear expressions may activate muscle units in preparation to facilitate scanning. We measured participants' eye movements during horizontal saccades to examine whether fear expressions are associated with increased eye-scanning speed relative to neutral expressions and whether fear expressions have opposing effects to disgust (see Methods). Employing the directed facial-action task, participants were prompted to pose a facial expression for 5 s while carrying out saccades between two circular targets separated by 27°. The facial actions for fear and disgust were modified to focus on eye configurations to accommodate an eye tracker and chin rest. Expression configuration had a significant effect on average velocity (measured in degrees of visual angle per second, $F_{2,38} = 18.001$, $P < 0.001$; **Fig. 4a**), increasing linearly from disgust to neutral to fear ($F_{1,38} = 33.975$, $P < 0.0001$). Although differences were small in magnitude, eye movements for fear expressions were reliably faster than those for neutral expressions ($t(19) = 2.133$, $P < 0.05$), and disgust expressions resulted in a more pronounced slowing relative to neutral ($t(19) = 4.42$, $P < 0.0003$). Peak velocity also differed between expressions ($F_{2,38} = 7.812$, $P = 0.001$), linearly increasing from disgust to neutral to fear ($F_{1,38} = 15.12$, $P < 0.0004$). A linear fit between the condition means ($r^2 = 0.99$) revealed that peak and average velocities increased from disgust to fear (**Fig. 4b**). Further analyses revealed that the amplitude (distance) of saccades differed across expressions ($F_{2,34} = 6.68$, $P < 0.004$), paralleling the linear increase from disgust to fear, which may have contributed to expression differences in velocity. However, we found that after equating for saccade distance, the above significant differences in velocity remained statistically reliable. Thus,

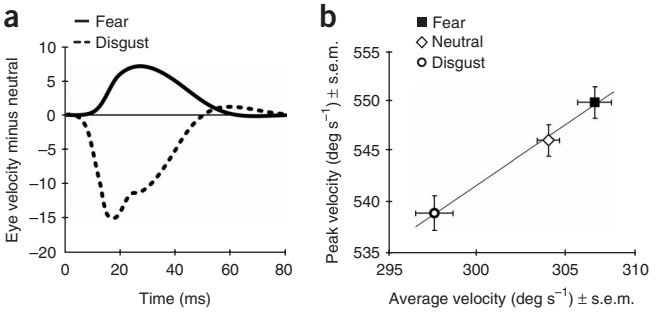

Figure 4 Saccadic eye movements for participants posing fear, disgust and neutral expressions. (**a**) Average velocity over time profiles for fear and disgust expressions relative to neutral. Relative velocities were scaled at each time point by the ratio of instantaneous-to-peak neutral velocity. (**b**) Average versus peak velocities for each condition are plotted along with the best-fit line between the condition means ($r^2 = 0.996$) with within-subject error bars.

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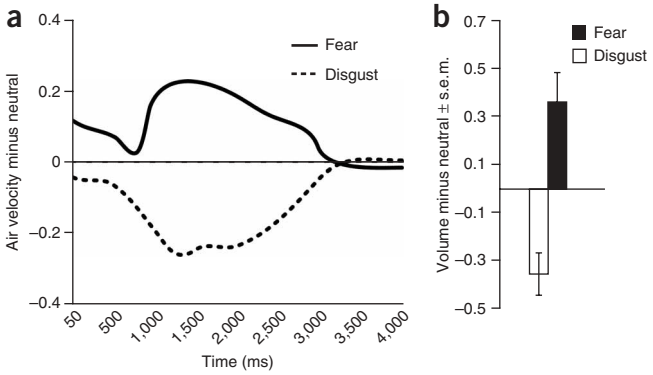

Figure 5 Measurement of nasal inspiratory capacity during expressions of disgust and fear. (**a**,**b**) Mean air-flow velocity (in standardized units) for fear and disgust expressions relative to neutral during inhalation over time (2.2-s inhalation; **a**) and mean volume relative to abdominal-thoracic respiratory effort (in standardized units) for disgust and fear expressions relative to neutral (**b**). Velocity was scaled such that the area under the curve for neutral sniffs was equal to 1.

in addition to altering visual-field size, facial actions of fear and disgust enhance and decrease the speed of horizontal foveation during target localization, respectively.

The above studies focused on the function of facial actions in the upper region of the face. We next examined the functional consequences of facial actions associated with the mid-lower region of the face by examining whether expression appearance may also relate to more primitive chemosensory functions. Disgust has been proposed to originate in defensive reactions related to the rejection of noxious chemical stimulation, whereby sensory exposure is reduced to potential contaminants[25]. According to the principle of form, fear configurations should serve the opposing action of disgust. We examined whether fear and disgust facial expressions regulate the entry of airborne substances to the olfactory mucosa through one of the most basic and primitive forms of sensory intake, nasal inspiratory capacity[36] (see Methods).

Facial expression was manipulated via the directed facial-action task, while nasal respirometry, nasal temperature and abdominal-thoracic respiratory measures were acquired during a controlled instructed breathing cycle (2.2 s in/out per breath). Expression configuration had a significant effect on air intake ($F_{2,36} = 9.93$, $P < 0.0005$), linearly increasing from disgust to neutral to fear ($F_{1,36} = 19.73$, $P < 0.0001$). Despite equal duration of inspiration, fear was associated with an increase in air velocity and volume corrected for respiratory effort relative to neutral expressions ($t(18) = 2.30$, $P < 0.04$; **Fig. 5a**,**b**). In contrast, disgust was diminished relative to neutral ($t(18) = 2.34$, $P < 0.04$). To ensure that these effects were not artifacts of the effect of expression on airflow measurements with a nasal respirometry mask, we further examined inspiratory-related temperature changes under the nostrils with a wire nasal thermistor. This revealed an identical pattern ($F_{2,34} = 12.07$, $P < 0.0001$), showing a linear effect of expression ($F_{1,34} = 23.57$, $P < 0.0001$), with fear expressions being associated with greater temperature change relative to neutral ($t(17) = 2.77$, $P < 0.02$) and disgust being diminished relative to neutral ($t(17) = 2.07$, $P = 0.05$).

Altered air intake may reflect a variety of factors rather than genuine structural changes in sensory capacity afforded by facial expression form. We next sought to determine whether visible surface deformations of the face (that is, facial expression appearance) are associated with invisible underlying structural changes of the internal anatomy of the nasal passages. In an additional control study, we examined directly whether fear and disgust altered the structure of the nasal passages in opposing manners. High-resolution fast spoiled gradient–recalled (FSPGR) magnetic resonance images of the nasal passages were acquired during the directed facial-action task (see Methods). Nasal volume depended on expression ($F_{2,72} = 14.98$, $P < 0.0001$), which was most evident in the more inferior aspects of the nasal passages

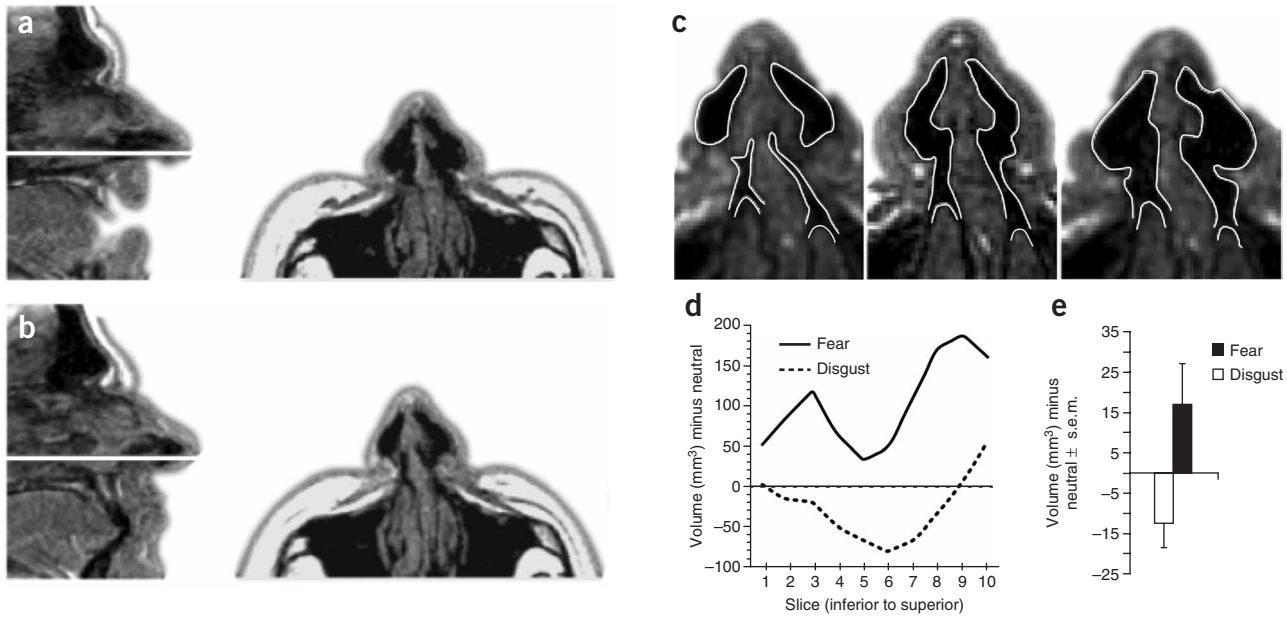

Figure 6 Effects of fear and disgust expressions on internal nasal anatomy. (**a**,**b**) Axial slices from T1-weighted FSPGR MRI during fear (**a**) and disgust (**b**) expressions. (**c**) Passageways to the inferior turbinate of the respiratory mucosa. Relative to neutral expressions (middle panel), disgust (left) and fear (right) expressions resulted in closure and dilation, respectively. (**d**) Plot of the volume of air cavity of the ventral portion (12 mm) of the nasal passages for fear and disgust expressions relative to neutral. Each slice was 1.2-mm thick with an in-plane resolution of 0.86 × 0.86 mm. (**e**) Bar graphs represent average overall air cavity volume for fear and disgust expressions relative to neutral.

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($F_{6,72} = 22.15$, $P < 0.0001$). Paralleling the inspiratory psychophysical results, nasal passage volume was linearly related to expression ($F_{1,72} = 29.68$, $P < 0.0001$); fear was associated with increased volume relative to neutral ($F_{1,72} = 10.06$, $P < 0.003$) and disgust was associated with decreased volume relative to neutral ($F_{1,72} = 5.19$, $P < 0.03$; **Fig. 6**). Closer inspection of these structural images revealed that fear expressions further resulted in a dilation of the entry to the inferior nasal turbinates of the respiratory mucosa, consistent with horizontal mouth stretching and lowering facilitating nasal passage dilation; in contrast, disgust resulted in a sealing off of this normally open passage (**Fig. 6c**), consistent with upper lip raising and nose wrinkling.

DISCUSSION

In contrast with suggestions that humans are endowed with an intricate facial musculature for the purposes of social communication[1], here we examined the idea that emotional expressions not only signal emotions, but may have originated to modify preparedness for perception and action. Specifically, we sought evidence for Darwin's principles of expression opposition in form and function[15]. Fear and disgust were shown to be near opposites in form, supported by fundamentally opposing action tendencies. Evidence of enhanced visual-field size, saccadic velocity and nasal inspiratory capacity in fear and the direct inverse in disgust indicate that there is a parallel opposition in function between the two expressions, serving the functions of sensory vigilance to enhance detection of the source of potential threat[19] and sensory rejection to reduce sensory exposure[25]. As our experiments focused on a subset of expressions, our results do not preclude the possibility that expressions other than fear and disgust are shaped by sensory function or whether fear and disgust are the prototypical manifestations of this selection pressure. Nevertheless, our findings provide evidence that is consistent with the possibility that facial expressions originate in egocentric sensory function rather than allocentric communicative value, indicating that the varieties of facial expression form may be shaped by a common underlying sensory regulatory function.

Our results cannot demonstrate that expressions are necessarily adaptive for the sender and may be argued to have limited direct functional importance. For example, the enhanced effects of fear in the visual perimetry experiments were confined to the upper visual field, and the associated increases in eye-movement velocity for fear were relatively small compared with the reductions in disgust. The perception and action effects were also small compared with the large opposition in form between fear and disgust. That is, fear and disgust are judged to be highly discriminable signals of emotional state compared with their consequences for perception and action. This is consistent with the notion that, under conditions of careful observation, one can measure a residue of their origin as an adaptive action tendency, despite the more robust present day use of facial expressions as social signals. The smaller egocentric effects of sensory intake relative to the larger allocentric effects of expression discrimination may then reflect that these expressions contain only vestiges of an evolutionary action tendency gating sensory intake[15].

Changes in facial musculature are thought to generate an afferent signal to the brain that causes changes in emotional experience[11,12,37]. According to such facial feedback theories, one potential account of our findings is that the directed facial-action task engages CNS representations of fear and disgust to alter perception and action. In contrast, expression form may directly gate exposure of sensory surfaces to augment or diminish sensory intake. With regard to expression form, facial feedback accounts do not explain the strong antithesis between fear and disgust as shown by our statistical model of expression appearance. With regard to expression function, our results demonstrate that changes in the degree of eye opening resulted in measurable increases to the visual field in fear and decreases in disgust. Furthermore, structural magnetic resonance imaging (MRI) revealed opposing actions of opening versus closing of the nasal cavities, consistent with increases in the capacity for nasal inspiration in fear and decreases in disgust. These convergent sources of evidence suggest that facial expressions are configured to alter the biomechanical properties of the face directly, rather than indirectly gating sensory exposure through facial feedback to the brain.

That fear and disgust are opposed in appearance may be an adaptation solely toward enhancing their discriminability as social signals. However, it is unlikely that the antagonistic spreading-contracting facial actions underlying expressions of fear and disgust occur because these facial configurations are best adapted to convey these states, as the reverse mapping (that is, displaying fear expressions during disgust and vice versa) would serve this communicative function equally well. These actions would also serve to reverse their sensory consequences (for example, enhancing sensory exposure in disgust). This gives purpose as to why, in contrast with verbal language, where symbols and meaning are arbitrarily related[38], facial expressions contain systematic relations in their appearance[26,27], demonstrating substantial similarity across cultures[7,39] and in the sighted as well as the congenitally blind[40,41]. Such results suggest that innate appearance relations among facial expressions and their associated meanings may rest on an evolutionarily older and more primitive foundation of expression production in sensory function.

Nonhuman primates close their eyes and flatten their ears as part of the innate protective startle reflex, which serves to reduce exposure of the sensory organs[2]. Such reflexes have come to serve important communicative functions[42]. We suggest that human facial expressions similarly originated in an innate functional capacity to alter sensory processing and sensory exposure. These functional adaptations may have been co-opted, serving as a preadaptation that is critical for human social-emotional communication. Over time, the functional and signal value of expressions have probably co-evolved such that the functional importance for the sender is coupled with the communicative importance for the receiver. As such, despite their proposed nonsocial origin, facial expressions may be maintained for their newer role in social communication[15] and may even be further shaped by culture for this purpose[42]. However, this more dominant present day role of expressions for social communication does not necessarily explain why they arose in the first place.

Although the spreading-constricting source of physical variance revealed by the vector flow field analyses is critical to fear and disgust, it probably represents a fundamental dimension of facial action that underlies all expressions[16]. There are components of fear and disgust that are shared with other expressions (for example, the eye and mouth opening is common to fear and surprise, and brow lowering is common to disgust and anger). This view is consistent with the component process model of emotions[28], whereby emotions are thought of as constellations of subcomponents that are not unique, but are shared across emotions. These subcomponents represent distinct stimulus evaluation checks or appraisals by the organism. With respect to eye opening, this would lead to increased detection and facilitated eye gaze toward a novel or unexpected stimulus, which, as our results have shown, is characteristic of fear. If this increased sensory phase reveals that the stimulus is aversive or of immediate threat, this might result in the activation of a defensive response repertoire[28] that closes off the senses to avoid exposure to the stimulus, which is characteristic of disgust.

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This conception of facial expression form and function as varying along a dimension of sensory vigilance and rejection may have implications for theories of facial expression mimicry. Emotion recognition is associated with the mirroring of facial motor actions, which has been proposed to represent a mechanism for socially sharing mental states and emotional experience[10,13]. In addition to this role in social communication, the sensory regulation hypothesis suggests that facial expression mimicry may originate in an underlying functional action resonance, whereby the sensory functional benefits of facial expression for the expressor are passed on as preparatory action tendencies to observers. For instance, with regard to fear expressions, this facial action resonance may have bestowed nearby observers with enhanced perception and action toward localizing potential threats in the environment.

Although we demonstrate that expression function is an important dimension of expression form, it is unlikely that expression utility is restricted to altered sensory intake. Facial expressions have probably been shaped to maintain stereotyped appearance in ways that do not alter sensory fitness. Expression appearance may contribute to an emotion's unique phenomenological experience[11,37]. Expressions may also be configured to mimic paedomorphic features, rendering the expressor more juvenile in appearance and thus less threatening[43]. There are multiple natural and cultural selective pressures that influence expression appearance. Despite these many influences, we suggest that the principle of antithesis in form, which long ago may have originated as a sensory adaptation, is employed more generally as an algorithm for efficient social-emotional communication, enhancing discrimination, whether that be in communicating well-being (for example, up- versus down-turned lips in smiles versus frowns) or social status (raising versus lowering the head in pride versus shame[44]). Facial expression form, even for the most social of emotions, may then be originally shaped by forces from our hominid evolutionary past[15,45] to regulate sensory exposure and intake. The form and function of facial expressions in the present day probably reflect these dual pressures, enhancing fitness in navigating the physical and social environment.

METHODS

Opposition in facial appearance. We implemented a computer graphics–based facial appearance model using the active appearance model framework commonly applied to computer vision[30] to investigate characteristic variations in facial appearance that are important for representing photorealistic facial expressions (see **Supplementary Methods** online for model details). Faces were represented by the model as vectors of shape and surface reflectance features. Expression prototypes were constructed by averaging the feature vectors for each face in an expression category and generating an image from the average vector. The vector corresponding to a prototype codes variations from the mean face that are common to all face exemplars in a given expression category, such as shared elongation or contraction of combinations of facial features. Antiprototypes were constructed by multiplying the elements of an average prototype vector by –1 to reflect the vector about all of its axes. Hence, antiprototype faces are computational and visual opposites from their corresponding expression prototypes[31].

Face stimuli. To train the appearance model, we collected face stimuli from the Japanese and Caucasian facial expressions of emotion (JACFEE) dataset[29] depicting six basic emotions (anger, disgust, fear, happiness, sadness and surprise). Eight face exemplars (4 males and 4 females) were selected for each of the six basic emotions for a total of 48 faces.

Behavioral ratings of prototypes and antiprototypes. Participants, 18 undergraduate students, viewed and rated four categories of facial expression prototype: fear, disgust, antifear and antidisgust. For each expression category, three different exemplars were presented, corresponding to a female prototype face, a male prototype face and an overall prototype face generated from the appearance model. Each face was rated on different emotion rating scales (intensity from 1 to 7) comprising anger, disgust, fear, happiness, sadness and surprise. Faces were presented in a random order until each exemplar was rated on each of the rating scales. The ratings for the three exemplars from each expression category were averaged within participant to determine a single score for each of the expression types.

Directed facial-action task. For experiments examining sensory function, participants engaged in a directed facial-action task. To produce disgust facial configurations similar to those in the JACFEE dataset that employed the facial action coding system[29], we instructed participants to raise their upper lips, wrinkle their noses and raise their cheeks. To produce fear facial configurations, we instructed participants to raise their brows as high as they could and draw them together, raise their upper eyelids, let their mouths drop open and stretch their lips horizontally. Participants were instructed to relax their facial muscles to achieve the neutral pose. An experimenter provided coaching as needed to help the participants comply with the instructions. During practice, a digital web camera was placed in front of the participants to record facial activity. The camera and its output screen were adjusted so that participants could see their own faces. As we employed objective measures of sensory-motor capacity, with the exception of the subjective visual-field procedure, no attempts were made to disguise the emotional content of the expressions configured in the directed facial-action task.

Subjective visual-field estimation experiment. Participants, 20 undergraduate students, were instructed to pose fear and disgust facial configurations, employing the directed facial-action task, while they were positioned in front of an elliptical representation of their visual field on a 44 × 34-inch grid with horizontal, vertical and two oblique axes. Participants stood approximately 12 inches (30 cm) from the grid and were asked to maintain their gaze on a central fixation point. After each trial, participants indicated on an 8.5 × 11-inch version of the grid the observed changes in their visual-field size relative to that of the neutral expression by marking at each of eight eccentricities where the four axes intersected the ellipse (at 0°, 45°, 90°, 135°, 180°, 225°, 270° and 315°). This procedure was administered twice for each facial configuration and the order of presentation of the two configurations was randomized across participants. The units of the grid were 2 × 2 inches, which was the equivalent of approximately 9.5° of visual angle. Data were scored by counting the number of grid units that changed (positive or negative) from neutral. Participants were photographed during practice trials and the images were used to measure the distance between the upper and lower eyelids during disgust and fear poses to correlate with their perimetry judgments. These measurements were aligned rigidly across subjects from a set of eye landmarks positioned at the two eye corners, upper and lower lids, and the pupil, resulting in a commonly aligned set of aperture measures across participants and conditions.

Objective visual perimetry experiment. We instructed 14 undergraduate participants to pose fear, disgust and neutral facial configurations using the directed facial-action task while maintaining their gaze 8 inches away from a projection screen (150 × 111-inch projected image from a laptop). Participants were seated and stabilized on a chinrest as they fixated on a point at eye-level, at the horizontal center of the screen. A gray circle (1 inch in diameter) flashed in successive increments from outside the field of vision to the fixation point center, along five upper visual-field axes (0°, 45°, 90°, 135° and 180°). The circle approached in 1° visual-angle increments (1/2° for the 0° and 180° directions), appearing for 100 ms and disappearing for 100 ms at each increment. A 60-trial practice phase preceded the experiment to familiarize the participants and to calculate the average response times for stimulus detection (~300 ms). Participants were instructed to respond using a mouse button as soon as they detected something in their visual field, and the circle's visual angle from center at the time of the response was scored as the direction's eccentricity. In total there were 35 fear, 35 disgust and 70 neutral trials in ten counterbalanced fear and disgust blocks. We randomized 14 trials per block (five directions and two catch trials per expression), with fear and disgust trials always interleaved with neutral to minimize fatigue.

Eye-movement experiment. Twenty undergraduate students participated in this experiment. Expressions were modified to accommodate the use of a

chinrest and eye tracker. To produce disgust facial configurations, we instructed participants to only wrinkle their noses. To produce fear facial configurations, we instructed participants to raise their brows as high as they could and raise their upper eyelids. An Eyelink1000 eye tracker (SR Research) was used to record participants' eye movements at a 1,000-Hz sampling rate. The tracker was set up with a chinrest 58 cm from the tracking camera (1 degree of visual angle = 1 cm on computer monitor). An experimenter provided coaching as needed to help the participants comply with the instructions. Calibration and validation procedures were carried out to ensure that the tracker had a correct spatial frame of reference for each expression. For each trial, participants were instructed to either raise their brows and eyelids (fear), relax (neutral) or wrinkle their noses (disgust) and then press the space bar to perform the trial while holding the expression. Participants had to then shift their gaze as quickly and accurately as possible between two small blue circles (16-pixel radius) for 5 s. The circles were displaced horizontally 13.5 degrees to the left and right of the screen's center. Experimental trials alternated between fear and disgust. To limit fatigue, expression trials were always interleaved with a neutral expression trial. After two sets of four practice trials each, participants carried out 20 sets of experimental trials, which were identical to the practice trials in form, resulting in a total of 20 fear, 20 disgust and 40 neutral trials being recorded.

Nasal inspiration experiment. Twenty undergraduate students participated in this experiment. One participant had unavailable respiration data as a result of equipment failure and the nasal thermistor data were lost from an additional participant. Participants were instructed to pose fear, disgust and neutral facial expressions using the directed facial-action task.

For each posed-expression trial, participants were instructed to breathe in and out once while their respiratory activity was recorded. The instructed breathing cycle consisted of inhaling for 2,200 ms and exhaling for 2,200 ms, approximating the duration of the respiratory cycle during rest[46]. There were 20 alternating trials each of fear and disgust. Each expression trial was followed by a baseline comparison condition, during which the participants had to produce a neutral, relaxed facial configuration throughout the instructed breathing cycle. Only the respiratory measures recorded during the inhalation portion of the instructed breathing cycle tasks were submitted to analysis. A computer-based data-acquisition unit (Biopac MP 150) was used to collect the respiratory data and store the information on hard disk for offline analysis. Inspiratory volume was measured by a flow meter (medium-flow pneumotachograph transducer) attached to a face mask with an air-filled seal that was snugly secured by a head strap to prevent air leakage and a nasal thermistor placed under the right nostril. Inspiratory respiratory effort was measured by two strain gauges (pneumograph); one was attached circumferentially around the chest and the other around the abdomen (see **Supplementary Methods** for more details).

MRI of the nasal passages. A case study of the effect of expression on the structure of the nasal passages was undertaken by acquiring structural images while the participant maintained a prolonged facial expression (T1-weighted, oblique-axial, three-dimensional FSPGR; echo time = 2.5 ms, repetition time = 5.4 ms, flip angle = 25°, bandwidth = 31.25 kHz, matrix = 192 × 192 reconstructed on a 256 × 256 matrix, excitations = 1.00, field of view (FOV) = 22 × 16.5 cm, thickness = 1.2 mm, slices = 124, with a standard quadrature head coil). To increase signal-to-noise ratio in the off-center region of interest of the nasal cavity, a higher flip angle was used with only one signal average and no inversion recovery. The imaging protocol took approximately 2 min for each scan. Separate anatomical scans were acquired for the fear, disgust and neutral conditions. The posing of the expressions was undertaken using the directed facial-action task. There were approximately 5 min of rest time between each posed facial expression (see **Supplementary Methods** for more details.)

Note: Supplementary information is available on the Nature Neuroscience website.

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AUTHOR CONTRIBUTIONS

J.M.S. and A.K.A. contributed equally to this work. J.M.S. created and analyzed the facial appearance model and associated behavioral data. J.M.S. and A.K.A. collected and analyzed the structural MRI data. A.C. and W.G. collected and analyzed the respiration and visual-field data and wrote parts of the corresponding Methods sections. D.H.L. and R.F. collected and analyzed the objective perimetry data, and J.M.S. and R.F. collected and analyzed the eye-tracking data. J.M.S. and A.K.A. created the figures and wrote the final manuscript.

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